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Secondary Succession from Seed in Tropical Rain Forests

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Abstract

A review article on secondary succession from seed in large natural canopy gaps. The major part describes the seed biology of pioneer species — production and dispersal, the evidence for seeds in the soil, the nature of dormancy, and the stimulus to germinate. The last part gathers the evidence together and discusses heterogeneity in the establishment of secondary forest in natural gaps — temporal and spatial variations in the soil seed bank, triggers for germination, and differential establishment of species. Finally, the additional factors which operate in large gaps made by man (logging, burning, and repeated cultivation) are outlined.

Introduction

1972 saw the publication of two important papers from Mexico on tropical rain forests which have had a considerable influence (Gomez-Pompa *et al.* 1972: Guevara Sada & Gomez-Pompa, 1972).The nub of these papers was about the processes of regeneration in rain forests and the consequences of their present-day widescale destruction on an unprecedented scale. It was shown that in the forests of Veracruz on the Caribbean coast of Mexico there is a major disparity between the secondary species which regenerate from seed in the soil and the primary species which comprise the existing primary or climax forests. Secondary species are fewer in number than primary and most of them have a wide geographical range. The eventual replacement of secondary by primary species which restores climax forest after natural catastrophes may not happen if man has caused such extensive devastation that no primary species remain within range as seed sources. For this reason the authors described the primary rain forests as fragile. These two papers were soon augmented by a book in which a whole series of studies by various workers in the same forests near Los Tuxtlas were described (Gomez-Pompa *et al.*, 1976; see also Denslow, 1978).

The earliest experimental study on seed in rain forest soil was by Symington (1933), working in Malaya. Symington, a remarkably far-sighted botanist who died tragically young (Whitmore, 1976), had also demonstrated that seeds of secondary forest tree species occur under primary rain forest. A similar discovery was made in Nigeria by Keay (1960). Then, since the early 1970s, there have been investigations on many aspects of secondary succession in tropical rain forests. Information remains patchy but the desire to try to see general patterns is powerful and there have also been several reviews, more or less speculative depending on the state of knowledge and on the strength of the reviewer's desire to see a pattern.

Here one particular aspect of rain forest maintenance is reviewed — the studies made on secondary succession from seed that occurs in large canopy gaps. The review is set in context by briefer consideration of allied topics. The important fields of mineral nutrient cycling in secondary forest and the related but still largely speculative subject of the role of mycorrhiza are not discussed. The available evidence on these matters is reviewed by Harcombe (1980) and Snedaker (1980) and by Janos (1980, 1983) respectively. The results of ecophysiological studies on, for example, photosynthesis, growth patterns and rates, respiration and water relations are also omitted. The still very sparse information on these topics is variously discussed by Whitmore (1975, 1983), Bazzaz & Pickett (1980) and Lebrón (1980).

Tropical rain forests occur in those parts of the tropics where there is no dry season or only a very short one and tropical seasonal (or monsoon) forests replace them where the dry season is pronounced. There is a sequence of dry land forest formations which occur in progressively more seasonal climates. (Champion, 1936; Champion & Seth, 1968; Whitmore, 1975, 1983). There is no general agreement about where precisely to draw the boundary between rain and seasonal forests along this sequence of

formations which is why the term tropical moist forests introduced by Sommer (1976) to cover all rain and monsoon forest formations is so useful.

The studies reviewed here are mainly from tropical rain forests though some were made in places with a somewhat seasonal climate and may perhaps be best considered as tropical seasonal forests. In a few the importance of alternating wet and dry seasons on aspects of seed biology is manifest (Longman, 1969; Garwood, 1983 a & b; Swaine & Hall, 1983). One general matter on which we remain ignorant is whether there are systematic differences in secondary succession and its initiation between rain forests and seasonal (monsoon) forests.

The details of secondary succession in tropical rain forests are intricate. Simple concepts become blurred by the complexities of the real world. Nevertheless it is necessary to develop a conceptual framework to see how the intricacies interact and to identify areas of ignorance. But it should be remembered that there are alternative means to the same end and simplistic generalizations may be misleading.

2 Where secondary succession occurs

The forest canopy is continually changing as trees grow up, die and are replaced. Replacement is in canopy gaps. As a crude simplification it is found that in small gaps seedlings grow up which were already present because they had become established in the undergrowth shade. These are by definition shade-bearing or shade-tolerant. In large gaps shade-bearing seedlings die and the replacement forest is of trees which germinate after the gap is created. These are the so-called light-demanding, light-tolerant, pioneer or secondary tree species. Unlike the shade-bearers they cannot regenerate under a canopy, even their own, and depend for perpetuation on continually colonizing new large gaps. The species which colonize such gaps are replaced by shade-bearers. Species composition of the forest changes and eventually shade-bearers (climax species) which self-perpetuate *in situ* arrive. Primary forest has been restored. This process is secondary succession.

The model more or less fits observations but is rather crude and there are many nuances and unanswered questions. Research on 'gap-phase dynamics' in tropical forests has been reviewed by Denslow (1980b), Hartshorn (1980), Whitmore (1978, 1982) and Brokaw (in press).

It is interesting to note that some rain forest formations apparently lack a pioneer flora. Heath forest in west Malesia is not replaced in large canopy gaps by a distinctive suite of pioneer species. In an experimental clearing in a Kalimantan heath forest Riswan (1982) found regeneration was mainly by coppice shoots and that compared to evergreen rain forest there was much bare ground. Another example amongst the Eastern rain forests is that no distinctive secondary forest community has yet been demonstrated to replace those facies of primary ultrabasic forest which are floristically distinctive (see discussion in Whitmore, 1975, 1983). This could be through lack of careful observation.

Large canopy gaps are created naturally by windstorms or cyclones (Anderson, 1964; Whitmore, 1974; Crow, 1980), by earthquakes or landslides (Garwood *et al.*, 1979), or by the enlargement of small gaps by windthrow. Man also creates them artificially by felling forest for lumber or clearing it for cultivation of the land. Repeated cultivation, and the usually associated burning, can lead to soil degradation, including the loss of the surface layers and the roots and any seeds they contain; sites thus affected have a different secondary succession. Extreme degradation can lead to the replacement of trees by herbs, predominantly grasses. Nowadays timber extraction is usually by heavy machinery and often includes compaction of soil along trackways and the impoundment of streams to create waterlogged areas. In these ways man's destruction of the forest creates additional, unnatural conditions and secondary succession is overall more complicated — a topic to be discussed later. The main discussion now is about secondary succession in natural large gaps and a series of questions arises.

Stands of pioneer species (or nomads as he called them) were likened by van Steenis (1958) to scar tissue healing large wounds in the primary rain forest canopy. Pioneer species are rare in the primary forest itself and occur as solitary and usually large trees rather than as groups. Where do the stands of pioneers come from? As already stated, the first demonstration that seeds of pioneer tree species lie in the soil under the primary forest was by Symington (1933). This observation has now been repeated many times, the Mexican studies of Gomez-Pompa and Guevara Sada having triggered current interest in the whole subject of rain forest secondary succession. The next question is whether the seeds which germinate when a large clearing is created were already present after accumulating in the soil over a period of time as a **soil seed bank*** or **soil seed store*** or whether they arrived after the gap was created because of a more or less continuous **seed rain**. Symington's and then Keay's (1960) studies did not show whether the seeds they germinated had arrived at or after the moment of gap creation as seed rain or were already in the soil. In Symington's case the primary forest from which the soil came lay very close to potential seed sources in secondary forest. There are still rather few critical investigations on this point and these will be discussed later. If there is a soil seed bank, for how long can seeds survive and for how long do they survive in natural conditions where processes of decay and predation are active? Is the soil seed store (or indeed the seed rain) homogeneous in space and/or in time? What triggers germination

*(soil) seed bank and (soil) seed store are evocative phrases well-entrenched in the literature on both temperate and tropical ecosystems. Both 'seed bank' and 'seed store' used alone are ambiguous terms because they are also used to refer to man's artificial stores.

from the store and prevents it before gap formation? Are germination and then seedling establishment spatially uniform or do they vary from place to place? Do these processes vary at different seasons? In logged forest in Malaya it is observed that different patches of secondary forest have different groups of pioneer tree species. It has been argued (Whitmore, 1975) that this results from seeds of some species arriving first, establishing and thereby leaving no room for late arrivals. A knowledge of fruiting phenology would help determine the likelihood of this possibility. The alternative explanation is that seeds were present in the soil but conditions for germination and establishment differed from patch to patch. Both explanations are in fact equally likely on the evidence available and further data are required for resolution.

In some forests sucker shoots from roots and coppice shoots from broken (or cut) bole stumps contribute to the regrowth forest. This has been most studied in connection with recovery after man-made clearance, and will be considered later. Where sucker- or coppice-regrowth predominates secondary succession does not occur.

3 Seed biology of pioneer tree species

3.1 Seed production and dispersal

The syndrome of characteristics of pioneer tree species is now generally agreed (van Steenis, 1941, 1958; Guevara Sada, 1974; Whitmore, 1975; Gomez-Pompa & Vazquez-Yanes, 1976; Vazquez-Yanes 1980b). These include the frequent, if not continuous, production of copious numbers of small seeds which are wind- or animal-dispersed.

3.1.1 Phenology

Continuous fruiting has been observed in *Trema guineensis** (Ulmaceae) (Longman & Jenik, 1974), *T. orientalis* (Stocker, 1981), *Cecropia obtusa* (Moraceae) and *C. sciadophylla* (Holthuijzen & Boerboom, 1982). Amongst twelve species of *Piper* (Piperaceae) in the Mexican Veracruz rain forests three in primary forest fruited annually, and, of seven confined to secondary forest, five fruited continuously and two annually; the remaining two species were variable in habitat and phenology (Vazquez-Yanes, 1976b). Frequent but not continuous fruiting appears to be the rule amongst the twenty secondary forest *Macaranga* species (Euphorbiaceae) of Malaya.

In Ghana most wind-dispersed pioneer species liberate their seeds in the dry season, particularly during February and March when the violent storms occur which are believed to be the most common natural causes of canopy-gap formation (Swaine & Hall, 1983). In primary subtropical lower montane moist forest in coastal Brazil Jackson (1981) found a peak in occurrence of wind-dispersed seeds at the end of the dry season. At Los Tuxtlas, in the Veracruz forests of Mexico, *Heliocarpus donnell-smithii* (Tiliaceae) produces its wind-dispersed fruits during the short annual dry season (Vazquez-Yanes & Orozco-Segovia, 1982a).

3.1.2 Dispersers

A wide spectrum of bird and bat dispersers, which increases the chances of successful dispersal, has been recorded for *Cecropia obtusifolia*. Seedlings of this species are very commonly germinated from soil samples (Vazquez-Yanes *et al.*, 1975). Cruz (1981) found in Jamaica that the submontane shrub or treelet *Dunalia arborescens* (Solanaceae) had 16 species of birds representing 14 genera and 8 families as dispersers.

At his Brazilian forest site Jackson (1981) found small seeds were produced less seasonally and were better dispersed than larger ones. He gave no indication of the seral status of the 227 species whose seed fall was monitored.

From a pantropical survey of the diet of frugivorous birds Snow (1981) distinguished several distinct classes of fruits. Frugivorous birds can be divided into opportunists and specialists. Fruits adapted to opportunists are typically small (5 – 10 mm), many-seeded, often showy and usually juicy. They provide mainly carbohydrates. Unlike opportunists, specialist frugivores are more or less completely dependent on a diet of fruits. Fruits adapted to them are often large, and are few- or single-seeded and oily. These two kinds of fruit characterize pioneer and climax plant species respectively. It would be revealing to explore these co-evolved syndromes more fully. Are pioneer trees mainly adapted to opportunist avian dispersers and climax trees to specialists as their fruit characteristics hint? Given that pioneers are commonly gregarious and fruit frequently or continuously what effect does this have on bird ecology?

3.1.3 Effectiveness of dispersal

This involves both the distance to which seeds are dispersed and whether dispersal is uniform or patchy. The area within which the seeds of a single tree fall is sometimes called its 'seed-shadow' a misleading term in so far as 'shadow' implies something negative, a screened area.

Ashton (1978) in Malaya germinated pioneer trees from soil taken from up to 500 m inside primary forest and also found considerable differences between different 1-m² samples. Cheke *et al.* (1979), working in Thailand, germinated pioneers from soil collected up to 175 m or more from the nearest putative parent. Hall & Swaine (1980) in Ghana germinated *Trema orientalis* from a site where the species had not previously been seen.

*authorities for species names follow the original publications.

Systematic studies of patchiness have been few. Bell (1970) only germinated 7 or fewer of a total of 13 species from any one of 6 forest sites in the El Verde lower montane rain forest, Puerto Rico, but as he points out, seed dispersal, survival or uneven germination could all have given this result. Direct observation of seed rain has been made by Fleming & Heithaus (1981) working in dry forest in Costa Rica. They found seeds below both the day and night roosts of frugivorous bats and deduced that the mixed species clumps of small-seeded secondary forest trees which occur result from such uneven dispersal. In contrast to this patchiness, uniformity was found by Hall & Swaine (1980) who obtained a quarter of all the pioneer species of Ghana in just 12 m² of soil from 6 forest sites, although there were minor differences related to climate and soil. In Sabah, Liew (1973) added few new species after sampling 5 milliacres (20.8 m²). Kellman (1970) deduced the seed rain to be uniform over an approximately 600-ha study area on Mindanao, with stands of pioneer species tending to be slightly more species rich near seed source areas, but made no direct study. Prevost (1981) directly observed the seed rain in French Guyana. She found seeds of *Solanum* spp. (Solanaceae) on the leaves of 18-month-old regrowth vegetation, and in the absence of nearby perches deduced that the seeds had been dropped randomly by flying birds.

The biological significance of the range of alternatives all these studies demonstrate will be elucidated either by comprehensive autecological studies of individual species, aimed to reveal how a particular set of attributes are integrated for a species to achieve success in its own particular ecological niche, or, alternatively, by comprehensive synecological investigations of particular forests.

3.2 Evidence for seeds in the soil

Seeds have now been germinated from primary rain forest soil in many parts of the tropics and on many occasions. The first direct, albeit qualitative, observation of the presence of viable seed appears to be that of Symington (1933), and the rapid appearance of seedlings in a large gap, sometimes within a week, has been deduced by many authors to indicate that seeds were already present. Guevara Sada & Gomez-Pompa (1972) suggest that the initial stages of secondary succession are already imprinted on a forest because of the soil seed store.

The studies nearly all show something more than simply the presence of seeds and it is more instructive to analyse them to categorize this extra information than simply to make a list.

3.2.1 Depth to which seeds occur

Brinkman & Vieira (1971), working near Manaus in Amazonia, considered there to be little seed buried below 5 cm. Enright (1978) observed at Bulolo, New Guinea, that pioneer species were absent from parts of logging areas where litter and topsoil had been scraped away and deduced that the soil seeds are held in these superficial layers. Holthuijzen & Boerboom (1982) in Surinam found the seeds of *Cecropia obtusa* and *C. sciadophylla* mainly in the top 1 cm. In fact the only study where seeds have been recovered from a considerable depth is by Cheke *et al.* (1979) who found them to 20 cm deep, at which level transition to subsoil began. This study was in lower montane rain forest and it is possible that soil-mixing earthworms (which are rare in the tropical lowlands) were present (see Collins, 1980), and had moved some seeds to an unusual depth.

3.2.2 Seed density

Many studies record total numbers of seedlings germinated from the small areas of soil tested. The depth and area of the sample varies between studies so results are not strictly comparable. Numbers are mostly very high. Typical values per square metre for primary forest soil are 355 (Hall & Swaine, 1980) and 60 to >300 (Prevost, 1981). Kellman (1974) found 6488/m² in agricultural land in Belize, mostly herbs and ruderals with *Cecropia peltata* and a single unidentified seedling the only trees. Holthuijzen & Boerboom (1982) found 73/m² of *C. obtusa* and *C. sciadophylla* under primary forest and Aubréville (1947) 498/m² of *Musanga cecropioides* (Moraceae) under a tall closed forest in tropical Africa.

An unexplored question relating to seed density is whether secondary forests develop a large soil seed bank of their component pioneer species which then progressively declines after the death of the pioneer parents.

3.2.3 Seed rain

A few researchers have obtained clear evidence that some of the pioneer regrowth in a large gap originates from seed rain, and not from seed already present at the time of clearing. Brinkman & Vieira (1981) showed that fire destroys seeds in the soil and deduced that seedlings which develop after slash and burn agriculture must therefore have been borne in. Enright (1978) noted that although some pioneer trees appeared very soon in his logging area at Bulolo others arrived later. By 18 months the initially bare tracks were being invaded by *Homalanthus novoguineensis* and *Mallotus* sp. (both Euphorbiaceae).Uhl *et al.* (1981) working in Amazonian Venezuela found that the first woody colonizers originated from the residual part of the soil seed store which had not been destroyed by fire, but forbs and grasses arrived soon after and were mainly wind borne.

Hall & Swaine (1980) made the interesting discovery that very few of the seeds in their soil samples were wind-dispersed. The implication is that wind-dispersed species arrive in seed rain and only animal-dispersed species occur as a soil seed store.

3.2.4 Evidence that seeds accumulate

Simply to germinate seeds from the soil gives no indication of the period over which the soil seed bank has accumulated. In the extreme case it could be of very recent origin. The available studies show that storage occurs for a range of periods and has no simple pattern.

Aikman (1955, in Lebrón, 1980) found that balsa (*Ochroma lagopus:* Bombaceae) seeds accumulated for several years. Schulz (1960) in Surinam observed germination of *Goupia glabra* (Celastraceae) seeds

within a few weeks of the primary forest canopy being removed, and at any time of year, although seeds were produced mainly between August and November. Guevara Sada & Gomez-Pompa (1972, 1976) germinated some pioneer species from most samples during most of the year whereas others were more local in space or time. Cheke *et al.* (1979) calculated that the seedlings germinated from their soil totalled more than one year's seed rain.

Stocker (1981), working in a subtropical rain forest in north Queensland, considered that only *Alphitonia petriei* (Rhamnaceae) had prolonged storage. Other species (both pioneers and shade-bearers) were observed to have low seed production most years and to be of limited viability. He also believed there to be considerable predation on the forest floor. Vazquez-Yanes & Orozco-Segovia (1982b) found that *Piper hispidum* seeds in the soil at Los Tuxtlas, Mexico, lost much of their viability in a year (but not when artificially stored moist in the dark). They attributed the extreme abundance of this species to its immense, continuous production of small, bird-dispersed seeds. Stocker (1981) attributed the success of *Trema orientalis* to the same causes. Vazquez-Yanes & Orozco-Segovia (1982a) discovered that at Los Tuxtlas, *Heliocarpus donnell-smithii* produces huge quantities of small, wind-dispersed, single-seeded fruits during the short dry season. These retained high viability for 12 months when buried in the forest at 5 cm depth in nylon bags.

These studies all suggest that storage may often be for only about a year. A few others provide firm evidence of longer viability in the soil. Lebrón (1979) at El Verde found that some seeds of *Palicourea riparia* (Rubiaceae) can remain dormant in the soil for at least three years. Buried seed of *Cecropia obtusa* and *C. sciadophylla* retained viability for 48 and 62 months respectively (Holthuijzen & Boerboom 1982). However, Kellman (1974) found no evidence for storage (mainly of herbs and ruderals) for over four years in agricultural soil in Belize.

The simple demonstration that seeds accumulate may by itself be of limited biological significance. Seasonal pattern in germination (and correlated differences in storage time) of likely adaptive value was found on Barro Colorado Island by Garwood (1983 a & b). Three quarters of seedlings emerged in the first three months of the rainy season. Those which are dispersed late in the rainy season or in the following dry season remain dormant in the soil until the next rainy season.

3.2.5 Artificial longevity

The length of time for which seeds can be stored under artificial conditions has sometimes been discussed in connection with the soil seed store, although it is only marginally relevant. Moreno Casasola (1976a) gave a comprehensive tabulation of storage trials of tropical tree seed, including the considerable compilation of Dent (1948) for Greater India which reported that a museum collection of *Ochroma lagopus* was still viable after 49 years.

Juliano (1940) in the Philippines buried seeds in glass vials — mainly those of herbaceous weeds but including a few shrubs and trees. The experiment was similar to a well known trial set up by J.S. Beal in the U.S.A. (in Darlington & Steinbauer, 1961). In these semi-natural conditions 11 species out of 21 were still viable at 6½ years. Ng (1980) tested the germination of 335 Malayan tree species in well-watered seed boxes within a shade-cloth enclosure and found that it was possible to distinguish (a) different periods before germination began and (b) different durations (from two weeks to two years) until it was complete. For both these parameters species lay along a continuum. Few of the species examined were true pioneers. About half had maximum viability of six weeks or less (typescript addition to reprints), but it is possible that the semi-natural conditions of these trials could for some species have led to unnatural behaviour.

Moreno Casasola (1976b) tested seeds of ten primary forest species from the Los Tuxtlas forest, Mexico, and found they had a short storage life. In the forest they germinated almost immediately. More generally, it is now known that many tropical rain forest trees have so-called recalcitrant seeds which not only have no natural dormancy but cannot have it induced for artificial storage. Many big fleshy seeds fall into this class. The other kind of seed which can be stored is called orthodox. Orthodox seeds are usually small. These two classes of seed were named by Roberts (1973). Whitmore (1983) discussed them for the Malesian rain forests and King & Roberts (1979) reviewed physiological knowledge on recalcitrants, which remains incomplete. Although no critical survey has yet been made, it is believed that tree species with recalcitrant seeds are primary forest shade-bearers and that pioneers have orthodox seeds. Van Steenis (1941) explicitly mentioned dormancy as a characteristic of pioneers.

3.2.6 Soil seed bank is mainly pioneers

Where experimenters have classified the species germinated from forest soil samples they have usually found that although most species are pioneers there are always a few shade-bearing primary forest species.

Guevara Sada & Gomez-Pompa (1972, 1976) and Moreno Casasola (1976b) germinated only a few primary forest seedlings belonging to only five species from the Los Tuxtlas primary rain forest soil. Liew (1973) germinated 1186 plants (31 species) from 20.8 m² of topsoil of which 730 belonged to 31 belukar (viz. pioneer) species and 61 belonged to 6 'jungle trees' viz. primary forest species. Hall & Swaine (1980) found that 90 per cent of species and 99 per cent of individuals from their Ghanaian soil samples were gap species. By contrast Schulz (1960) found at his Surinam forest sites that for none of the emergent primary forest tree species was seedling number increased by removing overhead shelter.

3.3 The nature of dormancy

It is beyond the scope of this review to discuss fully this major field of seed physiology (Khan, 1982). The range of phenomena discovered amongst tropical species is indicated by the following studies.

Trema guineensis has endogenous dormancy which naturally starts to disappear at 10 months but can be broken earlier by artificial stimulation with gibberellic acid or low temperature (Vazquez-Yanes, 1977). *Smilax coriacea* (Liliaceae) at El Verde only began to germinate after 6 months (Quaterman, 1970). In the same forests *Palicourea riparia* exhibited no germination for 2-3 months, and was variable through the population (Lebrón, 1979). *Belotia campbellii* (Tiliaceae) from Los Tuxtlas showed strong initial endogenous dormancy which slowly disappeared so that germination was progressive over 6 months (Vazquez-Yanes, 1981). Seeds of 12 Mexican *Piper* spp. exhibited different times until they started to germinate (Ludlow Weichers & Vazquez-Yanes, 1976). Ng (1980) found similar variability in his 10 per cent sample of the Malayan tree flora.

Induced dormancy was discovered in the West African tree *Hildegardia barteri* (Sterculiaceae) (Longman, 1969). It seemed likely that this was adaptive to climatic seasonality. Complex patterns of induced dormancy were discovered in the grass *Dactyloctenium aegyptium* by Longman (1969) and in the herb *Bidens pilosa* (Compositae) by Fenner (1980) working in East Africa.

For tropical rain forest trees the range of dormancy mechanisms remains very little known, even less so their likely ecological importance. The scattered observations have been collated by Vazquez-Yanes (1976b) and Bazzaz & Pickett (1980).

3.4 The stimulus to germinate

Important studies of considerable ecological significance have been made about the triggers for germination, and the earlier literature has been surveyed by Vazquez-Yanes (1976b).

Soil disturbance and removal of the forest canopy both alter the light, temperature and moisture regimes of the soil surface layers. From the experiments conducted so far light appears as the most important germination trigger, followed by temperature.

Soil disturbance, though by exactly what means was not ascertained, increased germination both in gaps and under forest at El Verde in experiments with the herbaceous weed *Phytolacca icosandra* (Phytolaccaceae) (Bell, 1970). In the same forest *Smilax coriacea* was found to germinate better on bare ground than litter-covered soil (Quaterman, 1970). Liew (1973) reported from Sabah that both the common pioneer tree *Anthocephalus chinensis* (Rubiaceae) and the abundant clearing climber *Mezoneuron sumatranum* (Leguminosae) were stimulated to germinate by soil disturbance.

Only germination experiments conducted in the forest or in conditions which simulate those encountered naturally can be ecologically interpreted. For this reason it is not possible to assess the significance of the discoveries of Castro Acuna & Guevara Sada (1976) and Lopez-Quiles & Vazquez-Yanes (1976). Experiments on supposed allelopathy, such as by Anaya Lang & Rovalo (1976), are notoriously difficult to interpret.

3.4.1 Light

Some species germinate in the dark and others require light. Blum (1968, in Vazquez-Yanes, 1980b) discovered that light is essential for *Cecropia obtusifolia, C. peltata, Trema micranthera* and *T. orientalis. Cecropia glaziovii* remained dormant in the dark (Valio & Joly, 1979) as did *Piper hispidum* (Vazquez-Yanes & Orozco-Segovia, 1982b). Longman & Jenik (1974) quoted an unpublished study that showed light is essential for the germination of *Chlorophora excelsa* (Moraceae), *C. regia, Mitragyna ciliata* (Rubiaceae), *Musanga cecropioides* and *Nauclea diderrichii* (Rubiaceae). Vazquez-Yanes (1976b) found no germination in 8 species in dark conditions. Of 12 Mexican *Piper* spp. 7 required light for germination but 5 germinated in the dark (Ludlow Weichers & Vazquez-Yanes, 1976). Moreover, within the species *Cecropia obtusifolia* 7 provenances required light to germinate but 2 more would germinate in the dark (Vazquez-Yanes, 1981).

3.4.2 Light quality

An important breakthrough was reported in a seminal paper by Vazquez-Yanes (1976a). He showed that light spectral composition controls the germination of *Piper auritum* and *Solanum diphyllum* (Solanaceae). Seeds were sown on agar and enclosed in boxes which were placed within the forest. In one set of boxes with a clear glass top, germination was zero. In the other, which had a red filter (640 nm), germination occurred. This demonstrated that the addition of red wavelengths to the light within the canopy is essential for germination, indicating the involvement of a phytochrome system. Light which has been filtered through a green leafy canopy is rather poor in red wavelengths and relatively richer in far red. With this balance of wavelengths germination is inhibited. In the open, red wavelengths are relatively richer and germination occurs. Subsequently other similarly photoblastic species have been discovered. The same response occurs in *Cecropia obtusifolia* and *Piper hispidum* (Vazquez-Yanes, 1979, 1980a). For *C. obtusifolia* and *P. auritum* experiments in growth chambers showed that short bursts of white light were inadequate for stimulating germination suggesting that seeds are sensitive to the difference between a passing sunfleck and a permanent canopy gap (Vazquez-Yanes & Smith, 1982). For *C. glaziovii* white light proved essential for seed germination although seedlings will grow under a canopy (Valio & Joly, 1979). For *Heliocarpus donell-smithii* a little germination occurred in the dark but more in white light though the main response in this species was to temperature, as described below (Vazquez-Yanes, 1981).

Several experiments have demonstrated little or no germination under a leafy canopy and good germination in the open. The same phytochrome system is deduced to be controlling germination. Schulz (1960) in Surinam found that pioneer species came up in large gaps in full light (and swamped primary species) although for none of the primary species did removal of the canopy increase their seedling numbers. Bell (1970) found 'explosive' germination in the open of several species at El Verde. Hall &

Swaine (1980) in Ghana found the majority of both individuals and species germinated from their soil samples in full light (2028 seedlings and 90 species against 120 and 25 in the shade). Fenner (1980) found germination of the weed herb *Bidens pilosa* was inhibited under leafy canopies. Aminuddin & Ng (1982), in the only study yet published from tropical Asia, studied *Sapium baccatum* (Euphorbiaceae), *Gmelina arborea* and *Vitex pinnata* (both Verbenaceae). Germination was complete in the open, zero under heavy shade and slight under light shade. It was deduced that there are two sorts of seed, one kind enabling regeneration of the species under a light forest canopy.

Another complex response was found for *Cecropia obtusa* and *C. sciadophylla* by Holthuijzen & Boerboom (1982). Germination was strongly triggered by white light but also occurred moderately in the dark when temperature fluctuated from 20 to 30°C. At El Verde *Palicourea riparia* germinated mainly in the shade while *Phytolacca icosandra* germinated where the soil was disturbed in both the open and under forest shade (Bell, 1970). *Piper hispidum* has the trigger to germinate only under a leafy canopy (Vazquez-Yanes & Orozco-Segovia, 1982b) viz. in light with a low red/far red ratio. This was confirmed by studies in growth chambers. The contrast to *P. auritum,* which needs the higher ratio found in white light, led these authors to deduce that the testa of *P. hispidum* has a particular optical property rather than the seeds having a different sensitivity to light.

3.4.3 Temperature

In contrast to soil under the canopy surface, the temperature of bare soil shows a considerable diurnal fluctuation and rises substantially at around noon. In Ghana, in a tropical moist semi-deciduous forest, the maximum temperature at 5 cm depth in a clearing was 31°C at 1300 hours compared with about 24.5° under the forest, and the minimum was 25° at 0500 hours compared with about 24° below the forest. At 20 cm depth in the clearing maximum temperature was only 27° and was reached later (1700 hours), the minimum was 25°; below the forest temperature remained fairly steady at about 23.5° (Lawson *et al.*, 1970). It can be expected that temperature in the top 1-2 cm where most seeds occur will be higher but measurements have apparently yet to be made.

Many years ago Aubréville (1947) reported that the pre-eminent West African short-lived pioneer tree *Musanga cecropoiodes* germinated from the soil seed bank in response to heating after canopy removal. The seeds have a hard testa and long viability and without heat are difficult to germinate. *Ochroma lagopus,* balsa, an important neotropical pioneer, also has temperature-sensitive seeds (Vazquez-Yanes, 1974, 1975; Vazquez-Yanes & Perez-Garcia, 1976) as has the sarmentose leguminous shrub *Mimosa pudica* (Lopez-Quiles & Vazquez-Yanes, 1976). For balsa, fire triggers simultaneous germination of seeds which have been accumulating slowly in the soil; without fire germination is sporadic. As fire also kills other seeds which co-occur in the soil fire favours balsa. The testa is waterproof, and scarification, especially at high temperatures, increases germination. In the laboratory, germination is vastly enhanced by momentary immersion in boiling water (Vazquez-Yanes, 1974). Edmisten (1970b) found that fluctuating temperature enhanced the germination of *Phytolacca icosandra* at El Verde. *Heliocarpus donnell-smithii* at Los Tuxtlas germinated best where soil temperature fluctuated through a diurnal range of 15°C and had a maximum of >31° for a few hours, although there was a little germination at constant soil temperature (Vazquez-Yanes, 1981; Vazquez-Yanes & Orozco-Segovia, 1982a).

Temperature may not act directly but by causing fluctuations in soil moisture. Taylor (1960) found in Ghana that germination of the large pioneer tree *Terminalia ivorensis* was poor but could be raised to 40 per cent by alternately drying and soaking the seeds one day at a time, for a week. This effect could be due to rupturing of the testa.

3.4.4 Testa rupture

This is a well-known prerequisite to germination for many Leguminosae. Whether it is equally important in pioneer and climax forest legumes remains to be discovered. Enhanced germination after digestion of the testa by a culture of the fungus *Rhizobium* was demonstrated by experiment with the El Verde tree *Ormosia krugii* (Papilionatae) (Edmisten, 1970a). Scarification enhanced germination of *Enterolobium cyclocarpum* (Mimosoideae) (Vazquez-Yanes & Perez-Garcia, 1977) and also of the El Verde pioneer herb *Phytolacca icosandra* (Edmisten, 1970b). The breaking of the dormancy of *Ochroma lagopus* by high temperature (previously discussed) is believed to result from rupture of the waterproof testa.

The ecological significance of every one of the germination mechanisms discussed here can only be assessed by carefully conceived and conducted forest experiment and observation.

4 Heterogeneity in the establishment of secondary forest

Secondary forest commonly varies from place to place and for many different reasons. In Section 3 we have shown that seed biology contributes various causes for spatial variation. It is useful to categorize these in order to clarify the points which still need investigating. Variation in secondary forest is often more complex where man created the gap. For this reason we shall consider natural gaps first.

4.1 Natural gaps

4.1.1 Soil seed bank

(a) *Temporal variation.* In at least some forests the soil seed bank at any place fluctuates with phenology and/or the longevity of seeds in the soil.

(b) *Spatial variation.* There have been a few direct demonstrations that dispersal of the seeds of pioneers into primary forest is not uniform. Rather more observations have shown differences from place to place in the seedlings germinated from different small surface soil samples. This probably (but not

necessarily) implies that the soil seed bank varies from place to place.

4.1.2 Triggers for germination

Amongst the handful of species studied, change in the light regime is the commonest trigger for germination, less common are changes in temperature, and other factors. This could, however, be simply because the light regime has been more frequently investigated than, for example, temperature and moisture effects.

It is conceivable, though not yet demonstrated, that germination triggers differ from gap to gap in natural forest, varying for example with size, and from the edge to the centre of a gap. This would result in a different fraction of a homogeneous soil seed bank being withdrawn by germination. Critical observations and experiments are needed.

The same germination triggers may affect species differently. Germination of species in sequence after gap formation, but sufficiently soon to make it likely their seeds were already in the soil, was observed in Sabah by Liew (1973), where species germinated in the experiment in much the same order in which they are known to occur in secondary succession. This was also observed in Kalimantan by Kartawinata *et al.* (1980) and Riswan (1982), and in French Guyana by Prevost (1981). The studies of Ng (1980) demonstrated different periods of innate dormancy after fresh seeds were sown in semi-natural conditions. The interaction of innate dormancy with naturally occurring triggers to germination has yet to be explored.

4.1.3 Differential establishment

Even if germination is homogeneous, seedlings of different species may establish with varying degrees of success. In an important study in the Venezuelan Amazon seeds of pioneer species were sown on six naturally occurring microsites. Most species tested had distinct preferences (Uhl *et al.*, 1981). In a subtropical rain forest at Mount Glorious, Queensland, establishment was observed to be not entirely homogeneous. *Homalanthus populifolius* was more common where the litter layer remained intact and *Phytolacca octandra* on bare soil (Williams *et al.*, 1969). More work on establishment requirements is needed. For example, are there systematic differences in microsite between the edge and centre of a gap or between gaps of different sizes?

Differential establishment also remains poorly studied in primary rain forest. Differences for seedlings of Dipterocarpaceae between granite- and shale-derived soils were discovered by Burgess (in Whitmore, 1975, 1983). Burgess also found that peat seemed to be an absolute bar to dipterocarp establishment. On the Malayan main range peat accumulates from 1050 m upwards and so is probably the principal factor limiting the altitude attained by this important family.

(a) *A herb stage.* The conditions which lead to the occurrence or dominance of a herb stage before the establishment of woody seedlings are not understood. General observations suggest that it may be favoured by disturbance by man additional to tree felling. Grasses are often common and may predominate. In experiments with forest soil at Los Tuxtlas weeds sometimes swamped tree seedlings (Lopez-Quiles & Vazquez-Yanes, 1976). At Bulolo, the grass *Paspalum dilatatum* was common in certain areas four months after logging (Enright, 1978). In their bulldozed clearing in Queensland Williams *et al.* (1969) found that the initial vegetation comprised two successive fluxes of annual herbs. In his felled and burned plot in Queensland, Stocker (1981) found that germination began after about one month and included herbaceous weeds with a few grasses. During the second year grasses increased greatly and by 23 months dominated most of the area between regenerating trees. At their site in Venezuelan Amazonia, Uhl *et al.* (1982) found that forbs and grasses dominated early succession after farm abandonment, but by one year woody species were common.

So far this review has concentrated on succession initiated from seeds in natural large gaps. What differences are there where man has had other effects than simply imitating nature by the felling of trees?

4.2 Large gaps effected by man

4.2.1 Man's various effects

Primitive logging involves the felling of scattered trees which are dragged out by man or his animals, elephant, buffalo, mule or pony, sometimes after being sawn into baulks. The effect is not dissimilar from natural gap creation.

Modern logging almost invariably uses wheeled or tracked machinery. Usually more stems are removed per hectare. Certainly more are damaged. The machines disturb the soil litter layer and the top soil with the roots and any seeds it may contain. Large areas are scraped bare, soil is compacted along trackways and swampy areas may be created. Perhaps damage or removal of the soil surface is the single factor which contributes most to the observed differences in secondary succession which occur on such areas (Whitmore, 1983). A modern logging area is very heterogeneous and contains patches of highly unnatural habitats. Study of forest recovery after logging is inevitably complex.

Any kind of agriculture involves burning as well as clearing. Fire is also a natural hazard in parts of the humid tropics, but in the wettest places, for example Malaya, very rarely affects primary rain forest. Prolonged cultivation may be associated with soil erosion, oxidation of soil humus, qualitative changes in the processes of decomposition, and leaching, viz. a general deterioration of the growing condition of the site.

In general it may be observed that secondary succession will be influenced by the history of the site, both by what occurred during forest clearance and by subsequent history. The discussion here is con-

cerned principally with the succession from seeds on degraded sites.

4.2.2 The effects of burning

(a) *Coppice.* Regrowth after felling by coppice shoots from cut tree trunks has been shown to be important in a few rain forests, usually coupled with the observation that fire after felling strongly reduces this vegetative reproduction. In his Queensland subtropical rain forest site, burned after felling, Stocker (1981) observed that by 23 months, 82 tree species were present, 74 as coppice shoots, 10 as shoots from root suckers and 34 from seeds. Uhl *et al.* (1981) found that fire killed many sprouts at their site in Venezuelan Amazonia. In Kalimantan, in evergreen rain forest after six months, burned plots had 122 species compared with 154 on comparable unburned plots; sprouts had decreased from 42 to 29 per cent. In a similar experiment in heath forest sprouts were almost eliminated by burning (Kartawinata *et al.*, 1980; Riswan, 1982).

The importance of the role of forest regeneration from sprouts needs more thorough investigation. There are implications for the floristic composition of regrowth forest. Perhaps such sprouts are commoner where trees have been artificially felled than after their natural demise.

(b) *Seeds.* Fire strongly reduces vegetative regrowth. It also reduces the soil seed store. Reduced species numbers in secondary forest grown on burned sites were reported by Kellman (1970) for Mindanao and in Kalimantan by Kartawinata *et al.* (1980) and Riswan (1982). Uhl *et al.* (1981) found that burning significantly decreased the soil seed bank and survival differed from species to species. In their experimental investigation near Manaus, Brinkman & Vieira (1971) buried seeds of 31 species then burned the area. The fire created temperatures of 100-150°C near the soil surface for several hours. By one month half the seeds had been killed by insects or fungi. At 2 cm depth all remaining seeds were killed by the fire. At 5 cm 80-100 per cent were dead but at 10 and 20 cm all seeds survived. This evidence suggests that usually all or most of the soil seed bank occurs in the top few centimetres and will be destroyed by the high temperatures that fire creates.

4.2.3 Repeated cultivation

It is beyond the scope of the present review to analyse the studies which document progressive site degradation under shifting agriculture where either the cultivation of a patch is prolonged beyond one or two seasons or where the 'bush fallow' period is shortened. In general, woody secondary species are eliminated by intensive agriculture and regrowth comes to be dominated by pantropical herbaceous weeds (Kellman, 1980; Uhl *et al.*, 1982). In Asia the aggressive regional variety *major* of the rhizomatous grass *Imperata cylindrica* invades after a few seasons' cultivation, and is difficult to eliminate. Anthropologists have come to realize that traditional shifting agriculturists know the value of the fallow period of secondary forest for sustained shifting agriculture on these intrinsically oligotrophic soils. They appreciate the importance of the sprout regrowth and the establishment of trees from seeds in their fields and know that this woody regrowth is diminished and eventually eliminated by continuing cultivation, weeding and burning for too long on a single patch (e.g. Driessen *et al.*, 1976, and Bayliss-Smith & Feacham, 1977, for Kalimantan and New Guinea respectively).

5 Conclusions

Until the early 1970s there was little critical or experimental work on the mechanisms for the re-establishment of primary rain forest in large gaps. Since then there have been substantial advances. A range of phenomena have been described.

The existence of a soil seed store and some of its characteristics have been demonstrated. Dormancy properties of tropical tree seeds have been studied, though the relative roles in nature of orthodox and recalcitrant seeded species remain largely speculative. Dormancy and germination have been studied in un-natural, semi-natural and natural conditions. A little work has been done on differential establishment in various sites and micro-sites.

There is much diversity in the processes involved in the establishment of secondary rain forest in large gaps. This review inevitably lacks focus because many of the processes are alternatives, existing within a broad general pattern.

Investigations which rely on reconstructing a temporal sequence from simultaneous studies on patches cleared at different times (e.g. Kellman, 1970) suffer the difficulty that past history is difficult to prove precisely and that with species-rich tropical floras there may be, even in one area, differences between patches despite identical treatments. More satisfactory are those studies which monitor a single patch through time, e.g. the Queensland Mount Glorious study (Williams *et al.*, 1969; Webb *et al.*, 1972) and the Kalimantan studies in evergreen rain and heath forests (Kartawinata *et al.*, 1980; Riswan, 1982). Secondary succession has been monitored on a single plot at Kepong, Malaya since 1948 (Kochummen & Ng, 1977) and was monitored for 18 years at Sungei Kroh, Malaya (Kochummen, 1966).

The dichotomy of rain forest trees into two groups of species, pioneer and climax, which underlies the analysis made throughout this paper, is too crude. In a review Denslow (1980a) recognized three groups, understorey, small gap and large gap. Whitmore (1974) recognized four responses to gaps amongst just twelve common large tree species on Kolombangara Island. Linked to the question of response to gaps for establishment is whether the tree flora of a given area contains a group of late secondary species (Budowski, 1970), intermediate between pioneer species (which start the secondary succession) and climax species (which perpetuate *in situ*). This query is in turn linked to another general question about forest succession. Do species of all stages start simultaneously (or nearly so) at the outset or do they establish sequentially, with species later in the succession developing below the pioneer canopy? Such sequential establishment was called relay floristics by Egler (1954). The twelve *Piper* spp. of the Mexican

Veracruz rain forests are depicted to arrive at different stages in succession (Gomez-Pompa, 1971; Vazquez-Yanes, 1976b) and dipterocarps take some years to invade secondary forest in Malaya (e.g. Kochummen & Ng, 1977). At Atewa, Ghana, Swaine & Hall (1983) discovered that most of the pioneer and climax species arrived during the first year, but that others continued to appear afterwards. The peak in numbers of pioneer species was reached in the third year but primary species were still arriving in the fifth year. In this study the pioneer trees were sub-divided into 'small' and 'large', short- and long-lived respectively (cf. Whitmore, 1975). The large pioneers also occurred in mature forest. The two Bornean studies reviewed in this paper both show sequential establishment of pioneer trees at the start of secondary succession (Liew, 1973; Kartawinata *et al.*, 1980), and this was also the case at Atewa (Swaine & Hall, 1983).

In planning studies in tropical rain forest, especially the effects of human disturbance, it needs to be remembered that the history of the site after clearance may have an important effect on secondary succession, as was found for the Hubbard Brook Forest of New England (Bormann & Likens 1979).

In the generalized crude model of gap-phase replacement described on p.768 it was depicted that in large gaps pre-existing shade-tolerant seedlings die from competition with the bigorous pioneers or from the sharp change in microclimate (which was monitored by Lawson *et al.*, 1970). It is also possible for them to be merely over-topped and to persist suppressed in the shade of the pioneers, eventually to replace them. Critical studies are required to elucidate the fate of shade-tolerant seedlings in particular forests.

I perceive a need now for detailed studies of secondary succession after precisely monitored different degrees of disturbance involving clearance, burning, and cultivation for one or more cycles. Best results will come from monitoring plots through time because uncertainties and additional complexities arise in any attempt to add together results from different plots. Succession in commercially logged forest will probably be the most difficult to understand because of the extra complexities such logging introduces. It will be useful to subdivide logged forest into areas with different kinds and perhaps also degrees of destruction. I also see a need for a more critical investigation into regeneration in natural forest gaps of different shape and size. We may perhaps agree with Denslow (1978) that 'understanding processes of secondary succession must come primarily from an appreciation of the variation in adaptive strategies of the species involved' and hope with her that this 'will lead eventually to enlightened management of these rapidly dwindling forests'.

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References

Aminuddin, M.; Ng, F.S.P. (1982) Influence of light on germination of *Pinus caribaea, Gmelina arborea, Sapium baccatum* and *Vitex pinnata. Malaysian Forester 45*, 62-68.

Anaya Lang, A.L.; Rovalo, M. (1976) Alelopatiá en plantas superiores: diferencias entre el efecto de la presión osmótica y los alelopáticos sobre la germinación y crecimiento de algunas especies de la vegetación secundaria de una zona cálido-húmeda de Mexico. In *Investigaciones sobre la regeneración de selvas altas en Veracruz, México [edited by Gomez-Pompa, C. et al.]* Mexico; Compania Editorial Continental, S.A. 388-427.

Anderson, J.A.R. (1964) Observations on climatic damage in peat swamp forest in Sarawak. *Empire Forestry Review 43*, 145-158.

Ashton, P.S. (1978) Crown characteristics of tropical trees. In *Tropical trees as living systems. The Proceedings of the Fourth Cabot Symposium held at Petersham, Massachusetts on April 26-30, 1976 [edited by Tomlinson, P.B.; Zimmermann, M.H.]* Cambridge, U.K.; Cambridge University Press. 519-615.

Aubréville, A. (1947) Les brousses secondaires en Afrique Equatorial. *Bois et Forêts des Tropiques.* No.2, 24-49.

Bayliss-Smith, T.P.; Feacham, R.G. (Editors) (1977) Subsistence and survival. Rural ecology in the Pacific. London; Academic Press. 428 pp.

Bazzaz, F.A.; Pickett, S.T.A. (1980) Physiological ecology of tropical succession: a comparative review. *Annual Review of Ecology and Systematics 11*, 287-310.

Bell, C.R. (1970) Seed distribution and germination experiment. In *A tropical rain forest. A study of irradiation and ecology at El Verde, Puerto Rico. USAEC Report* No. TID-24270 *[edited by Odum, H.T.; Pigeon, R.F.]* Oak Ridge, Tennessee; U.S. Atomic Energy Commission. D177-D182.

Brinkman, W.L.F.; Vieira, A.N. (1971) The effect of burning on germination of seeds at different soil depths of various tropical tree species. *Turrialba 21*, 77-82.

Brokaw, N.V.L. (in press) Treefalls, regrowth and community structure in tropical forests. In *Natural disturbance: an evolutionary perspective [edited by Pickett, S.T.A.; White, P.S.]* New York; Academic Press.

Bormann, F.H.; Likens, G.E. (1979) Pattern and process in a forested ecosystem. New York; Springer Verlag. xi + 253 pp.

Budowski, G. (1970) The distinction between old secondary and climax species in tropical Central American lowland forests. *Tropical Ecology 11*, 44-48.

Castro Acuna, R.; Guevara Sada, S. (1976) Viabilidad de semillas en muestras de suelo almacenado de "Los Tuxtlas" Veracruz. In *Investigaciones sobre la regeneración de selvas altas en Veracruz, México [edited by Gomez-Pompa, C. et al.]* Mexico; Compania Editorial Continental, S.A. 233-249.

Champion, H.G. (1936) A preliminary survey of the forest types of India and Burma. *Indian Forest Records (New Series), Silviculture 1*, 1-286.

Champion, H.G.; Seth, S.K. (1968) A revised survey of the forest types of India. Delhi; Manager of Publications. xxvii + 404 pp.

Cheke, A.S.; Nanakorn, W.; Yankoses, C. (1979) Dormancy and dispersal of seeds of secondary forest species under the canopy of a primary tropical rain forest in northern Thailand. *Biotropica 11,* 88-95.

Collins, N.M. (1980) The distribution of soil macrofauna on the West Ridge of Gunung (Mt.) Mulu, Sarawak. *Oecologia 44,* 263-275.

Crow, T.R. (1980) A rain forest chronicle: a 30 year record of change in structure and composition at El Verde, Puerto Rico. *Biotropica 12,* 42-55.

Cruz, A. (1981) Bird activity and seed dispersal of a montane forest tree *(Dunalia arborescens)* in Jamaica. *Biotropica 13* (Suppl.), 34-44.

Darlington, H.T.; Steinbauer, G.P. (1961) The eight-year period of Dr. Beal's seed viability experiment. *American Journal of Botany 48,* 321-325.

Denslow, J.S. (1978) mechanisms of succession in a tropical rain forest — a contribution from Mexico. *Ecology 59,* 862.

Denslow, J.S. (1980a) Gap partitioning among tropical rain forest trees. *Biotropica 12* (Suppl.), 47-55.

Denslow, J.S. (1980b) Patterns of plant species diversity during succession under different disturbance regimes. *Oecologia 46,* 18-21.

Dent, T.V. (1948) Seed storage with particular reference to the seed storage of Indian forest plants. *Indian Forest Records (New Series), Silviculture 7,* 1-134.

Driessen, P.M.; Buurman, P.; Permadhy, S. (1976) The influence of shifting cultivation on 'podzolic' soil from Central Kalimantan. *Bulletin, Soils Research Institute Bogor.* No. 3, 95-115.

Edmisten, J. (1970a) Some autecological studies of *Ormosia krugii.* In *A tropical rain forest. A study of irradiation and ecology at El Verde, Puerto Rico. USAEC Report* No. TID-24270 *[edited by Odum, H.T.; Pigeon, R.F.]* Oak Ridge, Tennessee; U.S. Atomic Energy Commission. B291-B298.

Edmisten, J. (1970b) Studies of *Phytolacca icosandra.* In *A tropical rain forest. A study of irradiation and ecology at El Verde, Puerto Rico. USAEC Report* No. TID-24270. *[edited by Odum, H.T.; Pigeon, R.F.]* Oak Ridge, Tennessee; U.S. Atomic Energy Commission. D183-D188.

Egler, F.E. (1954) Vegetation science concepts. I. Initial floristic composition, a factor in old field vegetation development. *Vegetatio 4,* 412-417.

Enright. N.H. (1978) The effects of logging on the regeneration and nutrient budget of *Araucaria cunninghamii* dominated tropical rain forest in Papua New Guinea. *Malaysian Forester 41,* 303-318.

Fenner, M. (1980) The induction of light requirement in *Bidens pilosa* seeds by leaf canopy shade. *New Phytologist 84,* 103-106.

Fleming, T.H.; Heithaus, E.R. (1981) Frugivorous bats, seed shadows and the structure of tropical forests. *Biotropica 13* (Suppl.), 45-53.

Garwood, N.C. (1983a) Seasonal rhythm of seed germination in a semideciduous tropical forest. In *The ecology of a tropical forest. Seasonal rhythms and long term changes [edited by Leigh, E.G. Jr.; Rand, A.S.; Windsor, D.M.]* Oxford, U.K.; Oxford University Press. 173-185.

Garwood, N.C. (1983b) Seed germination in a seasonal tropical forest in Panama: a community study. *Ecological Monographs 53,* 159-181.

Garwood, N.C.; Janos, D.P.; Brokaw, N. (1979) Earthquake-caused landslides: a major disturbance to tropical forests. *Science 205,* 997-999.

Gomez-Pompa, A. (1971) Posible papel de la vegetación secundaria en la evolución de la flora tropical. *Biotropica 3,* 125-135.

Gomez-Pompa, A.; Vazquez-Yanes, C.; Guevara [Sada], S. (1972) The tropical rainforest: a non-renewable resource. *Science 177,* 762-765.

Gomez-Pompa, A.; Amo Rodríguez, S. del; Vazquez-Yanes, C.; Butanda Cervara, A. (Editors) (1976) *Investigaciones sobre la regeneración de selvas altas en Veracruz, México.* Mexico; Compania Editorial Continental, S.A. 676 pp.

Gomez-Pompa, A.; Vazquez-Yanes, C. (1976) Estudios sobre sucesión secundaria en los trópicos cálido-húmedos: el ciclo de vida de las especies secundarias. In *Investigaciones sobre la regeneración de selvas altas en Veracruz, México [edited by Gomez-Pompa, C. et al.]* Mexico; Compania Editorial Continental S.A. 579-593.

Guevara [Sada], S. (1974) Recovery of tropical ecosystems. In *Fragile ecosystems [edited by Farnworth, E.G.; Golley, F.B.]* Berlin; Springer Verlag. *113-138.*

Guevera [Sada], S.; Gomez-Pompa, A. (1972) Seeds from surface soils in a tropical region of Vera Cruz, Mexico. *Journal of the Arnold Arboretum 53,* 312-335.

Guevara Sada, S.; Gomez-Pompa, A. (1976) Determinación del contenido de semillas en muestras de suelo superficial de una selva tropical de Vera Cruz, Mexico. In *Investigaciones sobre la regeneración de selvas altas en Veracruz, México [edited by Gomez-Pompa, C. et al.]* Mexico; Compania Editorial Continental, S.A. 203-232.

Hall, J.B.; Swaine, M.D. (1980) Seed stocks in Ghanaian forest soils. *Biotropica 12,* 256-263.

Harcombe, P.A. (1980) Soil nutrient losses as a factor in early tropical secondary succession. *Biotropica 12* (Suppl.), 8-15.

Hartshorn, G.S. (1980) Neotropical forest dynamics *Biotropica 12* (Suppl.), 23-30.

Holthuijzen, A.M.A.; Boerboom, J.H.A. (1982) The *Cecropia* seedbank in the Surinam lowland rain forest. *Biotropica 14,* 62-68.

Jackson, J.F. (1981) Seed size as a correlate of temporal and spatial patterns of seed fall in a neotropical forest. *Biotropica 13,* 121-130.

Janos, D.P. (1980) Mycorrhizae influence tropical succession. *Biotropica 12* (Suppl.), 56-64.

Janos, D.P. (1983) Tropical mycorrhizas, nutrient cycles and plant growth. In *Tropical rain forest: ecology and management [edited by Sutton, S.L.; Whitmore, T.C.; Chadwick, A.C.]* Oxford; Blackwell Scientific Publications (in press).

Juliano, J.B. (1940) Viability of some Philippine weed seeds. *Philippine Agriculturist 24,* 313-326.

Kartawinata, K.; Riswan, S.; Soedjito, H. (1980) The floristic change after disturbances in lowland dipterocarp forest in East Kalimantan, Indonesia. In *Tropical ecology and development [edited by Furtado, J.I.]* Kuala Lumpur; International Society of Tropical Ecology. 47-54.

Keay, R.W.J. (1960) Seeds in forest soil. *Nigerian Forestry Department Information Bulletin (New Series).* No. 4, 1-12.

Kellman, M.C. (1970) Secondary plant succession in tropical montane Mindanao. *Publication, Research School of Pacific Studies, Australian National University.* No. BG/2. 174 pp.

Kellman, M.C. (1974) Viable weed seed content of some tropical agricultural soils. *Journal of Applied Ecology 11,* 669-677.

Kellman, M. [C.] (1980) Geographic patterning in tropical weed communities and early secondary successions. *Biotropica 12* (Suppl.), 34-39.

Khan, A.A. (Editor) (1982) The physiology and biochemistry of seed dormancy and germination. Ed. 2. Amsterdam; Elsevier. 547 pp.

King, M.W.; Roberts, E.H. (1979) The storage of recalcitrant seeds — achievements and possible approaches. Rome; International Board for Plant Genetic Resources Secretariat [FAO].

Kochummen, K.M. (1966) Natural plant succession after farming in Sungei Kroh. *Malayan Forester 29,* 170-181.

Kochummen, K.M.; Ng, F.S.P. (1977) Natural plant succession after farming at Kepong. *Malaysian Forester 40,* 61-78.

Lawson, G.W.; Armstrong-Mensah, K.O.; Hall, J.B. (1970) A catena in tropical moist semi-deciduous forest near Kade, Ghana. *Journal of Ecology 58,* 371-398.

Lebrón, M.L. (1979) An autecological study of *Palicourea riparia* Bentham as related to rain forest disturbance in Puerto Rico. *Oecologia 42,* 31-46.

Lebrón, M.L. (1980) Physiological plant ecology: some contributions to the understanding of secondary succession in tropical lowland rain forest. *Biotropica 12* (Suppl.), 31-33.

Liew, T.C. (1973) Occurrence of seeds in virgin forest top soil with particular reference to secondary species in Sabah. *Malaysian Forester 36,* 185-193.

Longman, K.A. (1969) The dormancy and survival of plants in the humid tropics. *Symposia of the Society for Experimental Biology.* No. 23, 471-488.

Longman, K.A.; Jenik, J. (1974) Tropical forest and its environment. London; Longman Group Ltd. 196 pp.

Lopez-Quiles, M.; Vazquez-Yanes, C. (1976) Estudio sobre germinación de semillas en condiciones naturales controladas. In *Investigaciones sobre la regeneración de selvas altas en Veracruz, México [edited by Gomez-Pompa, C. et al.]* Mexico; Compania Editorial Continental, S.A. 250-262.

Ludlow Weichers, B.; Vazquez-Yanes, C. (1976) Germinación de semillas de *Piper hispidum* bajo diferentes condiciones de iluminación. In *Investigaciones sobre la regeneración de selvas altas en Veracruz, México [edited by Gomez-Pompa, C. et al.]* Mexico; Compania Editorial Continental, S.A. 263-278.

Moreno Casasola, P. (1976a). Viabilidad de semillas de arboles tropicales y templados: una revision bibliografica. In *Investigaciones sobre la regeneración de selvas altas en Veracruz, México [edited by Gomez-Pompa, C. et al.]* Mexico; Compania Editorial Continental, S.A. 471-526.

Moreno Casasola, P. (1976b) Latencia y viabilidad de semillas de vegetación primaria. In *Investigaciones sobre la regeneración de selvas altas en Veracruz, México [edited by Gomez-Pompa, C. et al.]* Mexico; Compania Editorial Continental, S.A. 527-548.

Ng, F.S.P. (1980) Germination ecology of Malaysian woody plants. *Malaysian Forester 43,* 406-437.

Prevost, M.F. (1981) Mise en évidence de graines d'espèces pionnières dans le sol de forêt primaire en Guyane. *Turrialba 31,* 121-127.

Quarterman, E. (1970) Germination of seeds of certain tropical species. In *A tropical rain forest. A study of irradiation and ecology at El Verde, Puerto Rico. USAEC Report* No. TID-24270 *[edited by Odum, H.T.; Pigeon, R.F.]* Oak Ridge, Tennessee; U.S. Atomic Energy Commission. D173-D176.

Riswan, S. (1982) Ecological studies on primary, secondary and experimentally cleared mixed dipterocarp forest and kerangas forest in East Kalimantan, Indonesia. *Thesis, Aberdeen University.*

Roberts, E.H. (1973) Predicting the storage life of seeds. *Seed Science and Technology 1,* 499-574.

Schulz, J.P. (1960) Ecological studies on rain forest in northern Suriname. Amsterdam; North Holland Publishing Co. 267 pp.

Snedakar, S.C. (1980) Successional immobilization of nutrients and biologically mediated recycling in tropical forests. *Biotropica 12* (Suppl.), 16-22.

Snow, D.W. (1981) Tropical frugivorous birds and their food plants: a world survey. *Biotropica 13,* 1-14.

Sommer, A. (1976) Attempts at an assessment of the world's tropical forests. *Unasylva 28* (112/113), 5-25.

Steenis, C.G.G.J. van (1941) Oecologische eigenschappen van pioniersplanten. *Tectona 34,* 557-567.

Steenis, C.G.G.J. van (1958) Rejuvenation as a factor for judging the status of vegetation types: the biological nomad theory. In *Study of Tropical Vegetation. Proceedings of the Kandy Symposium (1956) Humid Tropics Research.* Paris; UNESCO. 212-215.

Stocker, G.C. (1981) Regeneration of a north Queensland rain forest following felling and burning. *Biotropica 13,* 86-92.

Swaine, M.D.; Hall, J.B. (1983) Early succession on cleared forest land in Ghana. *Journal of Ecology 71,* 601-628.

Symington, C.F. (1933) The study of secondary growth on rain forest sites in Malaya. *Malayan Forester 2,* 107-117.

Taylor, C.J. (1960) Synecology and silviculture in Ghana. Edinburgh; Nelson & Sons Ltd. xi + 418 pp.

Uhl, C.; Clark, K.; Clark, H.; Murphy, P. (1981) Early plant succession after cutting and burning in the upper Rio Négro region of the Amazon basin. *Journal of Ecology 69,* 631-649.

Uhl, C.; Clark, H.; Clark, K.; Maquirino, P. (1982) Successional patterns associated with slash-and-burn agriculture in the upper Rio Négro region of the Amazon basin. *Biotropica 14,* 249-254.

Valio, I.F.M.; Joly, C.A. (1979) Light sensitivity of the seeds on the distribution of *Cecropia glaziovi* Snethlage (Moraceae). *Zeitschrift für Pflanzenphysiologie 91,* 371-376.

Vazquez-Yanes, C. (1974) Studies on the germination of seeds of *Ochroma lagopus* Swartz. *Turrialba 24,* 176-179.

Vazquez-Yanes, C. (1975) The use of a thermogradient bar in the study of seed germination in *Ochroma lagopus* Sw. *Turrialba 25,* 328-330.

Vazquez-Yanes, C. (1976a) Seed dormancy and germination in secondary vegetation tropical plants: the role of light. *Comparative Physiology and Ecology 1,* 30-34.

Vazquez-Yanes, C. (1976b) Estudios sobre ecofisiología de la germinación en una zona cálido-húmeda de México. In *Investigaciones sobre la regeneración de selvas altas en Veracruz, México [edited by Gomez-Pompa, C. et al.]* Mexico; Compania Editorial Continental, S.A. 279-387.

Vazquez-Yanes, C. (1977) Germination of a pioneer tree (*Trema guineensis* Ficalho) from equatorial Africa. *Turrialba 27,* 301-302.

Vazquez-Yanes, C. (1979) Notas sobre la ecofisiología de la germinación de *Cecropia obtusifolia* Bertol. *Turrialba 29,* 147-149.

Vazquez-Yanes, C. (1980a) Light quality and seed germination in *Cecropia obtusifolia* and *Piper auritum* from a tropical rain forest in Mexico. *Phyton 38,* 33-35.

Vazquez-Yanes, C. (1980b) Notas sobre la autecología de los árboles pioneros de rápido crecimiento de la selva tropical lluviosa. *Tropical Ecology 21,* 103-12.

Vazquez-Yanes, C. (1981) Germinación de dos especies de Tiliaceas arbóreas de la vegetación secundaria tropical: *Belotia campbellii* y *Heliocarpus donnell-smithii. Turrialba 31,* 81-83.

Vazquez-Yanes, C.; Orozco, A.; François, G.; Trejo, L. (1975) Observations on seed dispersal by bats in a tropical humid region in Veracruz, Mexico. *Turrialba 7,* 73-76.

Vazquez-Yanes, C.; Perez-Garcia, B. (1976) Notas sobre la morfología y la anatomía de la testa de las semillas de *Ochroma lagopus* Sw. *Turrialba 26,* 310-311.

Vazquez-Yanes, C.; Perez-Garcia, B. (1977) Notas sobre la morfología, la anatomía de la testa y la fisiología de las semillas de *Enterolobium cyclocarpum. Turrialba 27,* 427-429.

Vazquez-Yanes, C.; Orozco-Segovia, A. (1982a) Seed germination of a tropical rain forest pioneer tree *(Heliocarpus donnell-smithii)* in response to diurnal fluctuation of temperature. *Physiologia Plantarum 56,* 295-298.

Vazquez-Yanes, C.; Orozco-Segovia, A. (1982b) Germination of the seeds of a tropical rain forest shrub *Piper hispidum* Sw. (Piperaceae) under different light qualities. *Phyton 42,* 143-149.

Vazquez-Yanes, C.; Smith, H. (1982) Phytochrome control of seed germination in the tropical rain forest pioneer trees *Cecropia obtusifolia* and *Piper auritum* and its ecological significance. *New Phytologist 92,* 477-485.

Webb, L.J.; Tracey, J.G.; Williams, W.T. (1972) Regeneration and pattern in the subtropical rain forest. *Journal of Ecology 60,* 675-696.

Whitmore, T.C. (1974) Change with time and the role of cyclones in tropical rain forest on Kolombangara, Solomon Islands. *Institute Paper, Commonwealth Forestry Institute, University of Oxford.* No. 46, 92 pp.

Whitmore, T.C. (1975) Tropical rain forests of the Far East. Oxford; Clarendon Press. xiii + 282 pp.

Whitmore, T.C. (1976) Re-issue of a classic work on Malesian forest botany. *Taxon 25,* 629-630.

Whitmore, T.C. (1978) Gaps in the forest canopy. In *Tropical trees as living systems. The Proceedings of the Fourth Cabot Symposium held at Petersham, Massachusetts on April 26-30, 1976 [edited by Tomlinson, P.B.; Zimmermann, M.H.]* Cambridge, U.K.; Cambridge University Press. 639-655.

Whitmore, T.C. (1982) On pattern and process in forests. In *The plant community as a working mechanism [edited by Newman, E.I.] Special Publications Series of the British Ecological Society.* No. 1. Oxford, U.K.; Blackwell Scientific Publications. 45-59.

Whitmore, T.C. (1983) Tropical rain forests of the Far East. Ed. 2. Oxford, U.K.; Clarendon Press (in press).

Williams, W.T.; Lance, G.N.; Webb, L.J.; Tracey, J.G.; Dale, M.B. (1969) Studies in the numerical analysis of complex rain forest communities. III. The analysis of successional data. *Journal of Ecology 57,* 515-535.